Reviews

Propagation and release of natural enemies for control of cotton insect and mite pests in the United States*

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Abstract The state of the art for controlling four primary pests or pest complexes by augmentative releases of predators and parasitoids in the United States is reviewed. The pests are (1) the bollworm, *Helicoverpa zea* (Boddie) and tobacco budworm, *Heliothis virescens* (F.), (2) the boll weevil, *Anthonomus grandis grandis* (Boheman), (3) the pink bollworm, *Pectinophora gossypiella* (Saunders) and (4) plant bugs, specifically *Lygus* spp. Rearing of the predators and parasitoids and identification and the use of behaviour-modifying chemicals are described and discussed.

Keywords Cotton; biological control; augmentation; predators; parasitoids; propagation; natural enemies

Introduction

Damage attributed to insect and mite pests in United States cotton, which ranged from 7 to 14%, annually, during the last decade (Suguiyama and Osteen, 1988), occurred in spite of the best control efforts. In 1989, yields reduced by 9.2% resulted in a loss of 1.1×10^6 bales from potential yield and US$319 $\times 10^6$ in revenue. Additionally, the cost for insecticides and miticides to control the pests was US$266 $\times 10^6$, giving a total cost of US$685 $\times 10^6$ (King and Herzog, 1990).

These costs reduce the profitability of producing cotton in the United States, but producers have relied, and still are relying heavily, on synthetic pesticides to control arthropod pests (Herzog and King, 1990). These chemicals are relatively fast-acting, often control a complex of pests, can be used at a grower's discretion on a field-by-field basis, and generally are cost effective compared with alternative control methodologies.

Nevertheless, the availability of effective pesticides is declining precipitously. Many pesticides have been rendered obsolete because of resistance, and the United States public has become more and more alarmed about the safety of their food and water, as well as the impact of pesticide residues on animal and plant life threatened with extinction (King, Coulson and Coleman, 1988). Consequently, many chemicals have been banned, or their use restricted by the Endangered Species Act of 1973, which requires the Environmental Protection Agency (EPA) to protect endangered and threatened species under the Federal Insecticide, Fungicide, and Rodenticide Act. In addition, the costs of searching for new, effective compounds have escalated the cost of registering new chemicals to US$20–50 $\times 10^6$. Many chemicals registered before November 1984 are not being re-registered under EPA requirements because of putative chronic health effects and ground water leaching.

Finally, synthetic pesticides are petroleum based, and this non-renewable resource must be regarded as finite and in the long term alternatives are needed. The effects of synthetic pesticides on natural enemy populations with consequent elevation of secondary pests to primary pest status, previously innocuous arthropods to pest status, and pest resurgence, have renewed interest in the United States in the development of non-chemical methods for controlling arthropod pests. Certainly, biological control must receive high priority. Biological control involves managing natural enemies (restricted to predators and parasitoids in this paper) to reduce pest populations and their effects. Interrelated strategies are conservation, importation and augmentation: conservation is preservation of indigenous natural enemies; classical biocontrol involves importation for release and establishment where natural enemies are lacking; augmentation is propagation and release of natural enemies in selected areas where natural enemies are too sparse.

Integrated pest management

Biological control is an integral component of the cotton integrated pest management (IPM) strategy in the United

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States (King, 1986) – a system in which all available techniques are evaluated and consolidated into a unified programme for managing pest populations to avoid economic damage and minimize adverse side effects on the environment (National Academy of Sciences, 1969; Anonymous, 1984). For example, with regard to controlling the bollworm, *Helicoverpa* (= *Heliothis*) *zea* (Boddie) and the tobacco budworm, *Heliothis virescens* (F.), United States cotton insect control guides often provide a list of the predators that may be encountered while surveying insect pest infestations. Parasitoids are usually mentioned, but not by name. In many cases, these guides provide illustrations of important natural enemies. Typically, efforts are made to spare natural enemies by restricting insecticide applications, thereby maximizing pest suppressive action (King, 1986).

Avoidance of pesticide usage has often been cited as precluding the build-up of pest populations such as bollworm and tobacco budworm, aphids, whiteflies and mites because of pesticide-related mortality to the natural enemies (Bottrell and Adkisson, 1977).

Unfortunately, natural enemy populations often occur in too few numbers to prevent the build-up of pest arthropod populations to damaging levels. Certain pests such as the boll weevil, *Anthonomus grandis grandis* Boheman, plant bugs such as *Lygus* spp., the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), and the pink bollworm, *Pectinophora gossypiella* (Saunders), generally do not have effective natural enemies in cotton fields. Efforts have been made to import and establish effective natural enemies of these pests [boll weevil (Cate, 1985); plant bugs (Coulson, 1987); pink bollworm (Clausen, 1978; Legner, 1979)] as well as those of the bollworm and tobacco budworm (Powell, 1989), but these efforts have been unsuccessful.

E. F. Knipling (unpublished data, 1979) has developed numerous theoretical models demonstrating the technical feasibility of controlling pest populations by augmenting predator or parasitoid populations. Knipling (personal communication) conceptualized his thesis for augmentation as follows:

> Host-dependent parasites have evolved systems allowing reproduction without jeopardizing existence of the host. The coexistence patterns, in numerical terms, operate within rather narrow limits. However, addition of the parasites in sufficient numbers at strategic times can result in virtual elimination of the host.

The technical feasibility of propagating and releasing parasitoids and predators to control arthropods has been demonstrated repeatedly. This subject has been reviewed extensively (DeBach and Hagen, 1964; Ridgway and Vinson, 1977; King and Leppla, 1984; King *et al.*, 1985a; King, Hopper and Powell, 1985c). Van Lenteren (1986) has reviewed the augmentative releases of parasitoids in greenhouses. Greany, Vinson and Lewis (1984) have briefly reviewed the potential for using semiochemicals to manipulate parasitoids and the need for artificial culture techniques to mass propagate them. In general, the use of predators and parasitoids to control cotton pests was included in these reviews, but no review was devoted exclusively to this topic. Thus, the following discussion focuses on state-of-the-art control by augmentative releases of predators and parasitoids of four primary pests or pest complexes in the United States: the bollworm/tobacco budworm complex; the boll weevil; the pink bollworm, and plant bugs, specifically *Lygus* spp.

Table 1. Important parasitoids and predators of *H. zea* and *H. virescens*

Parasitoids	Predators
Microplitis croceipes	*Geocoris* spp.
Cardiochiles nigriceps	*Orius* spp.
Cotesia marginiventris	*Chrysoperla* spp.
Campoletis sonorensis	Coccinellids
Trichogramma spp.	Nabids
Eucelatoria bryani	Spiders

Control of the bollworm and tobacco budworm

Parasitoids

The principal parasitoids that contribute to mortality of bollworm and tobacco budworm eggs and larvae are shown in *Table 1*. Of these parasitoids, primary attention has been given to augmenting *Trichogramma* populations. More recently, major emphasis is being placed by three Agricultural Research Service (ARS) laboratories on the development of augmentative technology for the larval endoparasitoid *Microplitis croceipes* (Cresson). One laboratory is investigating the use of the tachinid, *Archytas marmoratus* (Townsend), and considerable progress at another laboratory has been made on the rearing *in vitro* of the tachinids, *Eucelatoria bryani* Sabrosky and *Palexorista laxa* (Curran).

Biological control of the bollworm and tobacco budworm in cotton by augmentative releases of *Trichogramma* in the United States, particularly *T. pretiosum* Riley, is comprehensively reviewed in King *et al.* (1985a). All aspects are reviewed, including rearing (Morrison, 1985a, b), transport, storage and parasitoid release technology (Bouse and Morrison, 1985), behavioural manipulation (Lewis, Gross and Nordlund, 1985), parasitoid movement (Keller and Lewis, 1985), efficacy (King *et al.*, 1985b; Lopez and Morrison, 1985), pesticide effects (Bull and Coleman, 1985), and modelling of augmentative releases (Goodenough and Witz, 1985). Another recent review is that by Olkowski and Zhang (1990), who list seven commercial producers of *Trichogramma* in the United States. These parasitoids are released over a total of ~81 000 ha. The parasitoid most commonly reared and released in cotton is *T. pretiosum*, and the Angoumois grain moth, *Sitotroga cerealella* (Olivier), is the host of choice.

The technical feasibility of suppressing bollworm and tobacco budworm populations in cotton by augmentative releases of *Trichogramma* has been repeatedly demonstrated in the United States (*Table 2*). P. D. Lingren and G. Kim (unpublished data) manually released 494 000 adult *Trichogramma* ha^{-1}, resulting in ~60% parasitism of bollworm and tobacco budworm for over a month in and

Table 2. Biological control of *H. zea* and *H. virescens* in cotton by augmentative releases of *Trichogramma*

Release rate (10^3 ha^{-1})	Parasitism (%)	Evidence of control	Reference
46–957	33–81	66–80% larval reduction	Stinner *et al.*, 1974
112–178	55–84	21% larval reduction	Jones *et al.*, 1979
110	15–90	Larval reduction	Ables *et al.*, 1979
47	42–80	Inadequate suppression	Luttrell *et al.*, 1980
413	28–60	31% increased yield	King *et al.*, 1985b

near the release area. Aerial releases of 123 500–247 000 adult *Trichogramma* ha^{-1} resulted in an average 51% parasitism of bollworm and tobacco budworm eggs on five Texas cotton farms (Ridgway, King and Carillo, 1977).

Stinner *et al.* (1974) evaluated the technical feasibility of reducing bollworm and tobacco budworm larval populations in cotton by releasing *T. pretiosum*. Parasitoid release rates were high (up to 957 000 ha^{-1}), but larval populations were suppressed. King *et al.* (1985b) reported three years of data following releases of *T. pretiosum* in cotton. In each year, egg parasitism was increased as a consequence of the release of parasitoids, but these parasitism rates could not be correlated with larval suppression. In the third year, parasitoid release plots yielded more cotton than untreated plots, although only 77% as much lint as from the insecticide-treated plots.

Perhaps the major factor limiting *Trichogramma* use for bollworm/tobacco budworm control in cotton in the United States is the preferential use of effective chemicals for controlling a complex of pests including plant bugs and the boll weevil. As *Trichogramma* is extremely sensitive to nearly all synthetic chemicals, its use is prohibited. This situation may change as chemicals become less available, boll weevils are eliminated as a pest from parts of the United States, and other non-chemical control strategies are developed. More research is needed to develop technology for managing parasitoids after release and for producing more vigorous parasitoids with longer life spans. Current procedures call for release of the parasitoid at rates exceeding 100 000 ha^{-1} at 3-day intervals during moth oviposition periods.

Larval parasitoids

Larval parasitoids are an important part of the environmental resistance to increase of bollworm and tobacco budworm populations. Unique complexes of hymenopterous and tachinid parasitoids have been recorded in various regions of the world (King and Jackson, 1989). Cumulative rates of larval parasitism are often high but the predominant species vary between regions of the country in the United States, as well as between crops (King, Powell and Smith, 1982). Special attention is given in this review to *M. croceipes*, one of the most important parasitoids of bollworm and tobacco budworm larvae in cotton and wild host plants in the United States (King and Powell, 1989). Over 50% parasitism of larvae was recorded during 1981 and 1982 in a series of cotton fields in the midsouthern United States despite application of insecticides.

Potential for using larval parasitoids in augmentative release has been indicated in small-scale tests. Lingren (1969) reported that *Cotesia* (= *Apanteles*) *marginiventris* (Cresson) had considerable potential for use in augmentative programmes. *Campoletis sonorensis* (Carlson), released at the rate of 680 day^{-1} for 10 consecutive days in a 0.2-ha cage (34 000 wasps ha^{-1} equivalent) infested with tobacco budworm larvae, resulted in 85% parasitization for 9 consecutive weeks (Lingren, 1977). Jackson *et al.* (1970) reported 58% parasitization of third-instar tobacco budworm larvae in cages when 2964 (equivalent) *M. croceipes* female wasps were released per hectare. Jackson *et al.* (1970) reported that if the tachinids, *E. bryani* and *P. laxa*, were released at the rate of 6175 female flies ha^{-1} on cotton containing 12 350 bollworm and tobacco budworm larvae ha^{-1}, ~50% parasitization should occur in 2 days.

Research on *M. croceipes* has been extensively reviewed (Powell, Bull and King, 1989). Basic biology, including host relationship physiology, was recently reviewed by Powell and Elzen (1989) and Vinson and Dahlman (1989). Behavioural aspects relating to habitat and host location, mate finding and mating were reviewed by Nordlund, Lewis and Tumlinson (1989), Elzen and Powell (1989) and Jones (1989). Other research vital to development of augmentative technology for *M. croceipes* is the effect of insecticides on the parasitoid (Bull, King and Powell, 1989), genetic characterization and genetic improvement (Steiner and Teig, 1989), and the possibility of developing a rearing system *in vitro* for the parasitoid (Greany, Ferkovich and Clark, 1989).

Hopper (1989) surmised that augmentation of *M. croceipes* as the principal parasitoid for control of the bollworm and tobacco budworm is technically feasible (King *et al.*, 1985c; King and Powell, 1989). On the basis of dramatically higher rates of larval parasitism, King, Powell and Coleman (1985d) hypothesized that *M. croceipes* was highly tolerant of many commonly used insecticides, particularly the pyrethroids. In general, the parasitoids are more tolerant of certain pyrethroids (e.g. esfenvalerate and cypermethrin) and carbamates (e.g. thiodicarb and oxamyl) and least tolerant of certain organophosphates (e.g. acephate and profenofos) (Powell and Scott, 1985).

M. croceipes prefers to parasitize third instars (Hopper and King, 1984b), but all parasitized instars move and feed less on the cotton plant (Hopper and King, 1984a); consequently, less damage is caused by parasitized larvae. Hopper, Powell and King (1991) report that releasing 2000 female *M. croceipes* ha^{-1} of cotton resulted in 75% parasitized bollworm and tobacco budworm larvae after 6 days, with an estimated 38% reduction in damage.

Growers possibly will not use *M. croceipes*, even if it could be mass produced, because apparently the presence of larvae feeding in cotton would not be tolerated, though feeding is reduced. Perhaps the best approach would be to release parasitoids on an area-wide basis while bollworm/tobacco budworm populations are still on early-season wild host plants along roadsides and field margins (Hopper, 1989). This area-wide suppression would provide

Table 3. Augmentative release of *Chrysoperla carnea* for biological control of *H. zea* and *H. virescens* in cotton fields[a]

Release rate (10^3 ha^{-1})	Larval reduction (%)
494	82
227	89
25	33
74	54
247	83

[a]Ridgway, King and Carrillo, 1977

an additive mortality factor to virus application, and parasitoids would search where the virus had not been applied.

Predators

No predators are currently being propagated and released for controlling the bollworm and tobacco budworm in cotton in the United States. Most management models do include predatory-caused mortality, at least indirectly, if not directly.

Releases of several hemipteran predators indicate that it might be feasible to augment their populations if economical procedures for mass producing them could be developed. Field-cage studies by Lingren, Ridgway and Jones (1968), van den Bosch *et al.* (1969), and Lopez, Ridgway and Pinnell (1976) with *Geocoris punctipes* (Say), *Nabis americoferus* Carayon, and *Podisus maculiventris* Say, respectively, demonstrate their ability to suppress bollworm and tobacco budworm populations in cotton.

Ridgway and coworkers demonstrated the technical feasibility of suppressing bollworm and tobacco budworm larval populations in cotton by periodic release of *C. carnea* eggs or larvae (*Table 3*). Release of 2- to 3-day-old larvae consistently produced significant reductions of bollworm and tobacco budworm populations on cotton. Reductions in bollworm and tobacco budworm larval populations were obtained by releasing as few as 247 000 *C. carnea* larvae ha^{-1}, and high levels of reduction were obtained in the field by releasing up to 494 000 ha^{-1} (Ridgway *et al.*, 1977).

Control of the boll weevil

Successful colonization of cultivated and wild cottons in Mexico enabled the boll weevil to move from its ancestral host, *Hampea*, and to migrate from its original distribution area in south-eastern Mexico and north-central South America to the United States (Burke *et al.*, 1986). Consequently, the boll weevil not only colonized a new resource, cotton, it also escaped natural enemies that had co-evolved with it and its ancestral host.

At least 55 indigenous parasitoid species are known to attack the boll weevil in the United States (Pierce, 1908; Hunter, 1910; Pierce *et al.*, 1912; Chestnut and Cross, 1971). These parasitoids characteristically have a wide host range and are facultative parasitoids of the boll weevil (Pierce, 1908; Cusham, 1911). Consequently, they do not respond to boll weevil population dynamics as would a more host-specific parasitoid. One of these parasitoids, *Bracon mellitor* Say, has been studied (Adams, Cross and Mitchell, 1969; Barfield, Sharpe and Bottrell, 1977), and is often recorded from field-collected, weevil-infested fruit (Bottrell, 1976). *Bracon mellitor* parasitism rates of the boll weevil can be high (Marlatt, 1933), and these rates are affected by cotton variety (McGovern and Cross, 1976; Adams *et al.*, 1969). However, its facultative host selection behaviour, failure to search the ground for weevil larvae, and preference for late-instar larvae, reduces its effectiveness (Meinke and Slosser, 1982; Cate, Krauter and Godfrey, 1990).

Cate and associates have identified at least 14 parasitoids attacking the boll weevil and a closely related species, *Anthonomus hunteri* Burke and Cate, in southern Mexico. Rearing techniques have been developed for several of these species (Cate, 1987). Nevertheless, all attempts to establish exotic natural enemies on the boll weevil in the United States beginning as early as 1895 (Townsend) have been unsuccessful (Cross and Chestnut, 1971).

One of the most promising exotic species is the pteromalid *Catolaccus grandis* Burks. The geographic distribution of this parasitoid is Mexico and southward but not in the United States. It was first described by Burks in 1954, but attempts to establish it in the United States have been unsuccessful (Johnson *et al.*, 1973; Cate *et al.*, 1990). In fact, Johnson *et al.* (1973) reported releases of *C. grandis* during 1967, 1968 and 1969, resulting in rates of parasitism ranging up to 72% as well as in-season recycling. Moreover, J. R. Cate and P. C. Krauter (unpublished, 1988) observed economic control of the boll weevil for a 6-week period after one release of 1200 females in early season cotton (cf. Cate *et al.*, 1990).

Based on the results reported by Johnson *et al.* (1973) and Cross and Chestnut (1971), E. G. King (unpublished) established a major effort at the ARS Subtropical Agricultural Research Laboratory, Weslaco, Texas, USA to assess the technical and economic feasibility of inoculating and augmenting parasitoid populations to suppress boll weevil populations. Following a planning workshop (in Weslaco, 1989), E. F. Knipling (Washington, DC, personal communication) developed a simulation model demonstrating that *C. grandis* may be used in biological control of the weevil. Subsequently, Morales-Ramos and King (1991) reported high rates of parasitism (up to 82%) of third-instar boll weevil larvae in cotton floral buds suspended near the plant terminal after release of 1500 *C. grandis* females from a central point in a 16.3-ha cotton field that was apparently devoid of a boll weevil natural infestation. In 1992, Morales-Ramos and coworkers (Morales-Ramos *et al.*, 1992) reported on large-scale propagation of *C. grandis* on boll weevil third-instar larvae in the laboratory, and Summy *et al.* (1992) reported up to 100% parasitism of boll weevil larvae by inoculated/augmented *C. grandis*, including elimination of reproduction. These studies are being continued and expanded.

Control of the pink bollworm

Several native predators and exotic parasitoids have been evaluated as potential candidates for augmentation against pink bollworm. Studies by Irwin, Gill and Gonzales (1974) suggested that most predators tend to be effective against the pink bollworm only at relatively high densities. Strategies have been developed to manipulate certain crops as field 'nurseries' for native predators, e.g. alfalfa (Stern *et al.*, 1967) and sorghum (Fye, 1971; DeLoach and Peters, 1972; Fye and Carranza, 1972; Robinson, Young and Morrison, 1972).

Bryan *et al.* (1973a, b) released $> 2 \times 10^6$ *Bracon kirkpatricki* and $\sim$280 000 *Chelonus blackburni* in $\sim$113 acres (46 ha) of Arizona cotton during 1972, and documented a significant reduction in the need for insecticidal treatment in release plots (one treatment for *Lygus* and one for pink bollworm) compared with control plots (four treatments for pink bollworm and one for the bollworm): parasitism by *B. kirpatricki* ranged up to 25% (which the authors considered an underestimate), whereas *C. blackburni* appeared to be largely ineffective (which the authors attributed to release in insufficient numbers). Later, Bryan *et al.* (1976) documented parasitism of $\sim$32% by *B. kirkpatricki* and $\sim$9% by *C. blackburni*, but concluded that such rates were insufficient to control pink bollworm.

Inundative release of several parasitoid species in the lower Colorado Desert of Arizona and California produced variable levels of pink bollworm control (Legner and Medved, 1979). Most effective was *Chelonus* sp. nr *curvimaculatus* Cameron, which was credited with an adjusted 69.6% reduction in infested bolls at the equivalent release rate of 2667 females ha^{-1} (Legner and Medved, 1979). The prospects of parasitoid augmentation as an effective control strategy have been enhanced by the fact that artificial diets and/or mass-rearing procedures have been developed for pink bollworm (Adkisson *et al.*, 1960; Stewart, 1984) and several of its associated hymenopterous parasitoids (Bryan, Jackson and Toner, 1969).

Control of *Lygus* spp.

Lygus are attacked by a wide range of predators and parasitoids, especially while on host plants other than cotton. A particularly effective predator of plant bugs is *Geocoris* spp. (Leigh and Gonzalez, 1976). High rates of egg parasitism (36%) by the mymarid, *Anaphes iole* (Girault) [= *A ovijentatus* (Crosby and Leonard)] has been recorded in cotton (Graham, Jackson and Debolt, 1986), but most studies indicate highest rates of parasitism in agriculturally undisturbed areas (Scales, 1973; Sillings and Broersoma, 1974).

Debolt (1987) discusses in some detail the potential for using augmentative releases of parasitoids to control *Lygus*. The development of an artificial diet for *L. hesperus* (Debolt, 1982) has made it possible to produce large numbers of host *Lygus* nymphs and eggs. An ARS Pilot Test is currently being conducted to assess the technical feasibility of controlling *L. hesperus* in alfalfa by augmentative releases of the mymarid egg parasitoid, *Anaphes iole* (Girault), and the braconid nymphal parasitoid *Leiophron uniformis* (Gahan). Control of *L. hesperus* in alfalfa would limit migration of the bugs into cotton after the plant is cut for hay or matures for seed production.

In small field plots in 1990, average egg parasitism rates of 57% were achieved with *A. iole* with single releases of 130 000 parasitoids (male and female) per acre. Average parasitism levels of 29% of the nymphs occurred following one-time releases of 22 000 female *L. uniformis* per acre (C. G. Jackson, personal communication, 1990).

Insect rearing

Efficient and cost-effective methods of rearing predators and parasitoids must be developed if augmentative releases are to be feasible (Beirne, 1974). Literally millions of natural enemies, available at rather unpredictable times, may be required for commercial augmentative releases. Finney and Fisher (1964) discussed problems associated with the culture of predators and parasitoids. Considerable attention has been paid to development of techniques to produce quality insects in large numbers (Smith, 1966; King and Leppla, 1984). The genetic implications of long-term laboratory rearing of insects are addressed elsewhere (Mackauer, 1972, 1976; Bouletreau 1986).

Powell and Hartley (1987) described techniques for manually producing large numbers of parasitoids efficiently. These authors adapted a multicellular host-rearing tray technique (Hartley *et al.*, 1982) to rear *M. croceipes* and several other species of parasitoids. The techniques, involving use of low-temperature storage, allowed simultaneous release of nearly 17 000 wasps. They noted several factors that were important for maintaining the rearing programme and which may be applicable to others. The quality of mass-reared insects also should be assessed (Boller and Chambers, 1977).

Our present inability to achieve mass propagation of parasitoids and predators of assured quality for a competitive cost is a major constraint to the augmentative approach in the United States. However, this may not pose a challenge in the near future as scientists (J. L. Roberson and D. D. Hardee) at the USDA Gast Rearing Laboratory, Southern Insect Management Laboratory, are coming closer to achieving automated mass production of *M. croceipes* (Powell and Roberson, 1992).

Commercialization may be practical only for selected organisms for which suitable diets and storage methods are developed. Artificial rearing is the 'breakthrough' that would potentiate practical use of augmentation for widespread pest control. Various groups have made progress in rearing of parasitoids *in vitro*, but a feasible system has yet to be developed. As many as 22 entomophagous species have been reared *in vitro*. Several Hymenoptera (one ectoparasite, four pupal parasitoid species, four species of *Trichogramma*) and three species of Diptera have been cultured, with varying success (King and Morrison, 1984). Predators, notably *C. carnea*, have been reared on artificial diets (Vanderzant, 1973; Martin, Ridgway and Schuetze, 1978).

Although there have been numerous successes in identification of oviposition stimulants or partial rearing (Nettles and Burks, 1975; Nettles, 1982), definitive development of a feasible rearing system for parasitoids *in vitro* has yet to be developed. Although considerable advances have been made in rearing *in vivo*, the advances have not been achieved to such an extent with rearing *in vitro*. The work of Wu and Junde (1984) illustrated an instance in which a completely synthetic artificial host egg was produced, which contains no insect derivatives and which supports *Trichogramma* oviposition and development.

Hymenopterous larval endoparasitoids have not been successfully reared to the adult stage on artificial diet. However, *C. marginiventris* and *M. croceipes* have been reared on artificial media through the first instar (P. Greany, personal communication). Larval endoparasitoids have evolved complex mechanisms that interact with the internal dynamics and organs of the host without damaging this environment or causing untimely demise of the host. The workings of these interacting factors must be understood at least minimally for rearing of larval endoparasitoids *in vitro* to become a reality (Thompson, 1986).

Development in rearing natural enemies on artificial diet may allow sufficient numbers to be produced for the further evaluation of natural enemies as biological control agents. An artificial diet that can be encapsulated has been developed for *Chrysopa*, and *G. punctipes* has been reared for more than 65 generations on an artificial diet (Cohen, 1992). In both cases, mass propagation requires significant engineering input.

Behavioural manipulation

A variety of behaviour-modifying chemicals (semiochemicals) affect the actions of predators and parasitoids in cotton and surrounding fields. These chemicals function at different trophic levels. In addition to chemicals from the parasitoid or predator and from the host or prey, chemical cues emanating from the host habitat affect the behaviour of the natural enemies. Moreover, chemical cues from the parasitoid or predator may be used in host seeking by hyperparasitoids. Understanding this complex chemical communication by parasitoids and predators, and between the different trophic levels, is critical for managing natural enemies and predicting levels of biological control.

Numerous kairomonal relationships between cotton arthropod pests and their natural enemies have been reported. For example, dispersal from the target area after augmentative release of predators or parasitoids often reduces the effectiveness of the augmentative approach. Provision of supplemental resources such as kairomones to attract, arrest, retain or stimulate the natural enemy to search more intensively for the host or prey could provide mechanisms for managing parasitoids and predators (Nordlund and Sauls, 1981). Tricosane and other hydrocarbons extracted from moth scales have been shown to increase parasitization by *Trichogramma* spp. (Jones *et al.*, 1973; Gross *et al.*, 1975). Oviposition-stimulating kairomones have been extracted from the accessory gland of the female bollworm (Nordlund *et al.*, 1987). The sex pheromone gossyplure, from the pink bollworm, caused increased parasitization of pink bollworm eggs by *T. pretiosum* (Zaki, 1985). Kairomones have been extracted from the frass of bollworm and tobacco budworm larvae that cause host seeking by the larval parasitoids *M. croceipes* and *Cardiochiles nigriceps* Viereck; one chemical identified was 13-methylhentriacontane (Jones *et al.*, 1971; Nordlund and Lewis, 1985; Heath *et al.*, 1990). A proteinaceous material found in the frass or haemolymph of tobacco budworm larvae stimulated larviposition by the tachinid *A. marmoratus* (Nettles and Burks, 1975).

Other behavioural chemicals, termed synomones because they facilitate location of the host by the parasitoid and consequently benefit the parasitoid and plant, have been found in cotton. The ichneumonid, *Campoletis sonorensis* Cameron, was shown to orient to and search host-free cotton plants (Elzen, Williams and Vinson, 1983). Host-searching behaviour by *C. sonorensis* (Elzen, Williams and Vinson, 1984) and *M. croceipes* (Nordlund and Sauls, 1981) increased on bollworm and tobacco budworm larvae fed on artificial diets, if cotton-plant material was put in the diet. Turlings, Tumlinson and Lewis (1990) discovered terpenoid volatiles from corn plants after feeding by *Spodoptera exigua* (Hübner) caterpillars, that attracted females of the parasitic wasp *Cotesia marginiventris* (Cresson) for host finding; they concluded that these terpenoids may be produced in defence against herbivores but may also serve a secondary function in attracting herbivore natural enemies.

Predators respond to many of the same chemical cues. Lewis *et al.* (1977) demonstrated an increased search rate by the common green lacewing, *Chrysoperla carnea* Stephens, on eggs of the bollworm when bollworm moth scales or extracts of the scales were applied to the search area. A compound in cotton, β-caryophyllene, was attractive to adult female green lacewings (Flint, Salter and Walters, 1979). Sabelis and Dicke (1985) summarized data showing that the phytoseid mite, *Phytoseiulus persimilis* Athias-Henriot, uses kairomones from its prey to locate it.

Conclusions

Much of the basic information required to implement biological control by augmentation in the United States is available. Enhanced knowledge on management of predator and parasitoid behaviour, coupled with use of genetically improved strains, will lead to increased effectiveness of biological control. The development of artificial diets and rearing procedures for parasitoids and predators *in vitro* will open the path for their mass production and commercial distribution for augmentative releases.

Over the next decade, social and environmental pressures in many countries will expedite implementation of technology for biological control of arthropod pests of cotton as well as other crops by propagation and augmentative releases of their natural enemies (predators and parasitoids). Their use will require careful integration with other techniques of cotton insect control. Certain pests, such as the boll weevil, heretofore resistant to biological control efforts, may be controlled by inoculative/augmentative releases of exotic natural enemies, although these natural enemies cannot be established.

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